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Historical considerations and comments on the type series of *Cyrtodactylus marmoratus* Gray, 1831, with an updated comparative table for the bent-toed geckos of the Sunda Islands and Sulawesi

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Abstract

Cyrtodactylus marmoratus Gray, 1831, a species of bent-toed gecko exhibiting a precloacal groove in males, was described on the basis of specimens collected by Heinrich Kuhl and Johan Conrad van Hasselt in Java, Greater Sunda Islands, Indonesia. Kluge (1985) subsequently designated a lectotype for *C. marmoratus* from a series of these specimens (i.e., syntypes), now housed in the herpetological collection at Naturalis (formerly the Rijksmuseum van Natuurlijke Historie; RMNH), Leiden, the Netherlands. Our work at Naturalis shows that the type series of *C. marmoratus* at RMNH actually comprises two sets of specimens, and that examination of specimens from one set or the other by different authors, including Kluge (1985), is responsible for some confusion surrounding the type series of this species. As a consequence, we present relevant morphological data for all 14 specimens constituting the type series of *C. marmoratus* at RMNH for the first time. The type status of two specimens of *C. marmoratus* in the collection at the Muséum National d'Histoire Naturelle, Paris, France, remains unresolved at present. Owing to the inconsistent naming and application of terms for some key characters (e.g., groove, sulcus, pit, hollow, depression) used in the diagnoses of *Cyrtodactylus* species, we here propose a set of novel and useful definitions that are supported by photographs. We also illustrate the sexually dimorphic expression of this character in *C. marmoratus*. Finally, we present a revised comparative table for the bent-toad geckos of the Sunda Islands and Sulawesi.

Key words: *Cyrtodactylus marmoratus*, bow-fingered geckos, Reptilia, Squamata, Gekkonidae, type specimens, paratypes, precloacal morphology

Introduction

Hartmann *et al.* (2016), as part of their recent description of *Cyrtodactylus klakahensis* Hartmann, Mecke, Kieckbusch, Mader & Kaiser, 2016, provided some further insights into the taxonomy of *C. marmoratus* Gray, 1831 and *C. fumosus* (Müller, 1895), two species hitherto considered to have fairly wide distributions in the Indonesian archipelago. Since this publication, we have uncovered additional information regarding the type series of *C. marmoratus* and some other species from the Sunda Islands and Sulawesi, which will be critical to the impending descriptions of additional species in the region (Awal Riyanto, in litt.; our unpubl. data). Furthermore, reporting on these new insights now also allows us to make some additions and corrections to the comparative table of Hartmann *et al*. (2016: Table 3) and prevent the perpetuation of omissions and errors in the next series of species descriptions from this region.

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Material and methods

Vouchers used to obtain data for our tables are listed in the Appendix. Measurements and scale counts follow Hartmann *et al*. (2016), unless stated otherwise. Comparative material is housed in the collections of the AMNH, BMNH, FLMNH, MCZ, MTD, NMB, RMNH, SMF, ZMA (now in Naturalis, Leiden; RMNH), ZRC, and ZSM (abbreviations follow Sabaj Pérez [2014]).

Results and discussion

A type series with two accession numbers

In a footnote referring to their comparison section (page 556: footnote 4), Hartmann *et al*. (2016) provided some meristic data for the lectotype of *Cyrtodactylus marmoratus* (RMNH.RENA 2710a.1), which differed from the values presented by Rösler *et al*. (2007). However, due to unclear numbering of specimens, it appears that Rösler *et al*. (2007) did not actually present data for RMNH.RENA 2710a.1, the lectotype, but for what they referred to as "RMNH 2710/1," a specimen they correctly called a paralectotype (Rösler *et al*. 2007: 206, Fig. 11). We compared our data for the lectotype of *C. marmoratus* to the data of Rösler *et al*. (2007), because we believed their notation "RMNH 2710/1" to be a variant of 2710a.1. This was an error on our part, rooted in the way the name-bearing specimens of *C. marmoratus* were partitioned at some point in the past, and in the unfortunate circumstance that the authors who collected data for two scientific articles covering *C. marmoratus* used only one set of specimens each, and moreover examined a different part of the type series.

Gray (1831) based his description of *Cyrtodactylus marmoratus* on a series of bent-toed geckos collected by Heinrich Kuhl (1797–1821) and Johan Conrad van Hasselt[1] (1797–1823) in Java and now housed in the collection of the Naturalis Museum (formerly the Rijksmuseum van Natuurlijke Historie, abbreviated RMNH) in Leiden, The Netherlands. Gray had examined these personally while visiting the RMNH collection (see Kluge 1985). Kluge (1985) subsequently designated an adult male (RMNH.RENA 2710a.1) as lectotype of *C. marmoratus*, rendering all other specimens of the original type series paralectotypes. The lectotype, now kept separately, came from a jar cataloged as RMNH.RENA 2710a, which contained a series of six specimens that Kluge considered to be the syntypes of *C. marmoratus*. Kluge listed no other types, even though a series of specimens cataloged under accession number RMNH.RENA 2710 existed.

Unfortunately, Rösler *et al*. (2007) based their species account of *Cyrtodactylus marmoratus* on specimens in the jar Kluge (1985) had not considered. The jar identified as RMNH.RENA 2710 contains eight specimens also collected by Kuhl and Van Hasselt in Java, and, in light of Kluge's (1985) paper, Rösler *et al*. (2007) correctly referred to them as paralectotypes (see below). Unaware that the reports by Kluge (1985) and Rösler *et al*. (2007) dealt with two distinct sets of specimens, we (Hartmann *et al*. 2016) felt it necessary to correct the counts made by Rösler *et al*. (2007) on the specimen they referred to as "RMNH 2710/1" (properly cited as RMNH.RENA 2710.1), which we thought must be the lectotype RMNH 2710a.1. We were then unaware (and we suppose Kluge was as well) that the type series of *C. marmoratus* at RMNH consisted of two sets of specimens under different catalogue numbers. Although Rösler *et al*. (2007: 205) listed the lectotype under its correct accession number in their note section for *C. marmoratus*, they appear not to have examined it, and therefore did not mention it specifically in their measurements and proportion section and their appendix. We feel that in a case such as this, where a divided type series exists but where only a single set (or subset of it) was examined in a study of broader implications, a direct reference to the other set(s) of the series is critical to prevent confusion. This appears especially important in the case an accession number itself gives no clear indication regarding partitioning. We assume that Kluge (1985) and Rösler *et al*. (2007), just like we ourselves, were stymied by the accession number scheme historically employed at the RMNH.

1. In the literature, Van Hasselt's second Christian name is often quoted as "Coenraad." Klaver (2007:43), however, demonstrated the proper name to be "Conrad."

What constitutes the entire type series?

We have now examined the entire type series of *Cyrtodactylus marmoratus* housed in the RMNH collection and note that all but three specimens had no individual labels, including all specimens in the jar labeled RMNH.RENA 2710. We were able to confidently identify the specimens enumerated by Rösler *et al*. (2007) as "RMNH 2710/1, 2710/2, and 2710/3" based on data and a photograph provided by these authors. These specimens have now received labels that correspond to the numbering of Rösler *et al*. (2007), identifying them as RMNH.RENA 2710.1, 2710.2, and 2710.3, respectively. Although, neither Kluge (1985) nor Rösler *et al*. (2007) explicitly stated that the type series of *C. marmoratus* at RMNH consisted of specimens in more than a single jar, Brongersma (1934) already reported on two series of specimens of *C. marmoratus* collected by Kuhl and Van Hasselt in Java (RMNH.RENA 2710, 2710a) but did not refer to them as types. We may assume that both sets of specimens (RMNH.RENA 2710 and 2710a), with the same data and collectors, were seen by Gray when he visited the RMNH in the late 1820s (Hoogmoed 1973). Absent any indication to the contrary, all must be regarded as types. By the time of Gray's visit, all material collected by Kuhl and Van Hasselt had been received in Leiden (Marinus Hoogmoed, in litt.), and both collectors had died (Klaver 2007). We present relevant morphological data for all 14 specimens of the RMNH type series in Table 1.

Brongersma (1934: 169) also referred to specimens of *Cyrtodactylus marmoratus* in the Muséum National d'Histoire Naturelle (jar number MNHN 2331) as syntypes ("collected in Java by Kuhl & Van Hasselt and preserved in the Paris Museum"[2]), whereas Guibé (1954) did not refer to these specimens at all in his catalogue of the lizard types in the collection of MNHN. Kluge (1985) stated that the specimens in the MNHN collection could not be treated as types without further consideration. Brygoo (1990) considered them types for four reasons:

(1) Duméril & Bibron (1836) and Duméril & Duméril (1851) stated that the Paris Museum received these two specimens from the Leiden collection (= RMNH);

(2) they were received prior to 1836 (the publication date of Duméril & Bibron's third volume of their *Erpétologie Générale*);

(3) Duméril & Bibron (1836) referenced Kuhl's unpublished manuscript (that contains a description of *C. marmoratus*) and Gray's (1831) valid species description;

(4) in his published catalogue, Gray (1845: 173) listed two specimens (*a*, *b*) that the Natural History Museum, London (BMNH) received from RMNH as well.

We dispute this assertion for the following reasons:

(1) In the 1820s and 1830s, the RMNH sent specimens to various museum collections, with vouchers of *Cyrtodactylus marmoratus* evidently transferred to the following institutions: BMNH—Gray (1845); MNHN—Brongersma (1934), Marinus Hoogmoed & Esther Dondorp, in litt.; NMW—Marinus Hoogmoed & Esther Dondorp, in litt.; SMF—Mecke & Kieckbusch, pers. obs. In the absence of records of an accession date for the Paris specimens (there are no extant records indicating the arrival of these specimens at MNHN; Nicolas Vidal, in litt.), there is no unique way by which these can be reliably connected to the collection made by Kuhl and Van Hasselt or the types in the RMNH.

(2) Depending on the year when these specimens were sent, they need not necessarily have been collected by Kuhl and Van Hasselt. After Kuhl's and Van Hasselt's deaths, there was a steady stream of young researchers (most of them dying very quickly after their arrival in the tropics) being sent out to Indonesia (e.g., Heinrich Boie, Heinrich Christian Macklot, Salomon Müller; and always via the main trading port of Batavia, now Jakarta, on Java) under the auspices of the Natuurkundige Commissie voor Nederlandsch Indië, and all material they collected went to the RMNH. There, specimens were partly or wholly accessioned, and then exchanges with other museums took place (Marinus Hoogmoed, in litt.).

(3) The references listed in Duméril & Bibron (1836) appear irrelevant to the question of type specimens in this case, given that these are merely taxonomic references associated with the species as a whole, and not with individual specimens.

2. Brongersma (1934), obviously unaware of Gray's species description, incorrectly attributed the authorship of *C. marmoratus* to Duméril & Bibron (1836), who worked at MNHN at the time when Kuhl and Van Hasselt material would have arrived in Paris (see Kluge 1985). Under this assumption it appears logical that Brongersma (1934) did not consider the specimen series RMNH.RENA 2710 and 2710a to be type material.

(4) The fact that Gray (1845) listed specimens of *Cyrtodactylus marmoratus* in the collection of the Natural History Museum, London (BMNH) indicates that these are most likely specimens that Gray had seen during his visit to Leiden and which were subsequently transferred to the BMNH (see Hoogmoed *et al*. 2010: 9 for a similar example). These specimens may be part of the original syntype series and hence paratypes. This information, however, lends no support to the assertion of type status for the MNHN specimens. If the MNHN specimens, now registered under the accession number MNHN 1994.0734 (Nicolas Vidal, in litt.), did once belong to the RMNH 2710/2710a series, Gray may have seen them either in Leiden (still as part of 2710 or 2710a) or in Paris in 1829 (see Bour 2006), depending on when the two specimens were sent to Paris. We feel that the MNHN specimens (and all other specimens of *C*. *marmoratus* that originated in Leiden) should not be regarded paralectotypes by default in the absence of specific indication of either collectors (which would have to be Kuhl and Van Hasselt) or an accession date; additional evidence is needed to confirm their status, but based on the archival research in Paris such evidence is likely not forthcoming (Nicolas Vidal, in litt.). We therefore follow Kluge (1985) to state that further consideration is required. Additional research on specimens of *C*. *marmoratus* that originated from Leiden is currently in preparation.

Of pores, grooves, sulci, pits, hollows, and depressions

Whereas Kluge (1985) counted 53 pores for the lectotype of *Cyrtodactylus marmoratus* (RMNH.RENA 2710a.1), we (Hartmann *et al*. 2016) reported 52. We re-examined the specimen and here correct the count to 56 pores, some barely visible. We also examined the two adult females from the type series (RMNH.RENA 2710.3, 2710a.6) and additional female specimens of that taxon, which show no sign of a precloacal groove or "shallow pit" as reported by Rösler *et al*. (2007) and possess a precloacal region largely different from that of males, which possess a groove. Rösler *et al*. (2007), however, referred to both expressions as "preanal pits." We refer the reader to Fig. 1 for a comparison of the precloacal region of a male and a female specimen of *C*. *marmoratus*.

It appears that the terms 'groove,' 'sulcus,' 'pit,' 'hollow,' and 'depression' are sometimes used interchangeably in the relevant literature but may also be used to refer to different expressions of depressed precloacal areas. These terms, used in combination with 'shallow' and 'deep' (as e.g., 'shallow sulci,' 'shallow pits,' or 'shallow depressions'), render this useful diagnostic character quite subjective. Harvey *et al*. (2015) divided this key character into two major categories based on their appearance, a longitudinal groove *vs*. a triangular depression, but neglecting the often used term 'pit.' We propose the following terminology: (1) A 'depression' can be of any shape and the term should be used as a higher category for the narrower terms 'groove' and 'pit.' A depression could therefore be present in the form of a grove or a pit, with the latter terms mutually exclusive. (2) A 'groove' is always longitudinal and relatively narrow. As part of a groove some or all of the scales (which are often pore-bearing) on the left and right side of the posterior-most, enlarged precloacal scale series are in contact with each other or only narrowly separated. This type of depression may have the shape of a slit (or sulcus) along its entire length, with the posterior-most precloacal scales often sunk deeply into the depression, being barely visible. Alternatively, these enlarged scales are arranged in the shape of an inverse 'Y' with the depression broadening posteriorly (Fig. 2A–C). (3) The term 'pit' (= 'hollow' *sensu* Hikida 1990) is used to refer to a triangular depression (*sensu* Harvey *et al*. 2015) with most or all of the scales (which are often pore-bearing) on the left and right side of the posterior-most, enlarged precloacal scale series widely separated from each other (Fig. 2D & E). Attribution of depressions to either a groove or a pit might be challenging, since transitional expressions may exist and/or because the shape of a depression may be affected by preservation. For these reasons, researchers should always depict the precloacal region of the bent-toed gecko taxa in question in order to give others a better idea of the described structures. The following species of *Cyrtodactylus* from the Sunda Island and Sulawesi possess a precloacal groove in adult males: *C*. *agamensis* (Bleeker, 1860); *C*. *cavernicolus* Inger & King, 1962; *C*. *celatus* Kathriner, Bauer, O'Shea, Sanchez & Kaiser, 2014; *C*. *fumosus* (Fig. 2C); *C*. *klakahensis* (Fig. 2B); *C*. *lateralis* (Werner, 1896); *C*. *marmoratus* (Fig.1A); *C*. *pubisulcus* Inger, 1957 (Fig. 2A); and *C*. *semicinctus* Harvey, O'Connell, Barraza, Riyanto, Kurniawan & Smith, 2015. The following species possess a precloacal pit in adult males: *C. baluensis* (Mocquard, 1890; Fig. 2D); *C*. *consobrinus* (Peters, 1871; Fig. 2E); *C*. *psarops* Harvey, O'Connell, Barraza, Riyanto, Kurniawan & Smith, 2015; *C*. *spinosus* Linkem, McGuire, Hayden, Setiadi, Bickford & Brown, 2008; and *C*. *yoshii* Hikida, 1990 (see also Table 2). Determination of the presence/absence of this character in *C*. *malayanus* (De Rooij, 1915) warrants further examination. The following species lack a depression: *C. batik* Iskandar, Rachmansah & Umilaela 2011; *C*. *darmandvillei* (Weber, 1890); *C*. *gordongekkoi* (Das, 1994); *C*. *hitchi*; *C*. *ingeri* Hikida, 1990; *C*. *jellesmae*; *C*. *laevigatus* Darevsky, 1964; *C*. *matsuii* Hikida, 1990; *C*. *petani*; *C*. *semiadii* Riyanto, Bauer & Yudha, 2014; *C*. *quadrivirgatus* Taylor, 1962; *C*. *wallacei* Hayden, Brown, Gillespie, Setiadi, Linkem, Iskandar, Umilaela, Bickford, Riyanto, Mumpini & McGuire, 2008; and *C*. *wetariensis* (Dunn, 1927; Fig. 2F).

TABLE 1. Metric (in mm) and meristic data from the type series of *Cyrtodactylus marmoratus* in the RMNH.RENA collection. RMNH.RENA 2710a.1 is the lectotype of *C. marmoratus*. RMNH.RENA 2710a.1–a.6 and RMNH.RENA 2710.1–3 are adults, 2710.4–8 are juveniles. Characters are abbreviated as follows: ArmL = arm length, AxialL = length from axilla to groin, DTR = dorsal tubercle rows, FP = femoral pores (number provided only when pore-bearing femoral scales are separated from pore-bearing precloacal scales by InfraS or when pores on the thigh are present only; a continuous pore series is referred to as PFP), GulS = gular scales (including second postmentals if present), HeadL = head length, HeadH = head height, HeadW = head width, InfraLab = infralabial scales, InfraS = infrascales (number of enlarged poreless scales separating pore-bearing precloacal from pore-bearing femoral scales), IOS = interorbital scale rows, LegL = leg length, LT_4 = subdigital scales/lamellae under fourth toe, OrbD = orbital diameter, PCT = postcloacal tubercles, PFP = precloacofemoral pores, PFS = precloacofemoral scales, PP = precloacal pores (number provided only when pore-bearing precloacal scales are separated from pore-bearing femoral scales by InfraS or when pores in the precloacal region are present only; a continuous pore series is referred to as PFP), PVT = paravertebral tubercles, SC = supraciliaries, SnoutL = snout length, SupraLab = supralabial scales, SVL = snout-vent length, TailL = tail length, VS = ventral scales. Regenerated tails were not measured with the condition abbreviated as 'reg.'. If data for a character are not available, this is indicated by a hyphen (-). A question mark (?) indicates an uncertainty in the absence/presence of a character. For specimens possessing precloacofemoral pores (= pores in a continuous series, including indistinct pores and primordia), precloacal- and femoral pores (separated from each other by infrascales) are coded as 'n/a'. In juvenile specimens pores are either located in the precloacal region only or run onto the legs. Discrepancies between the data for 2710.1–8 presented below and the data for this series presented by Rösler *et al.* (2007) may be due to different data collection methods.

Character	2710a.1 ♂	2710a.2 ♂	2710a.3 ♂	2710a.4 ♂	2710a.5 ♂	2710a.6 ♀	2710.1 ♂	2710.2 ♂	2710.3 ♀	2710.4 ♀	2710.5 ♂	2710.6 ♂	2710.7 ?	2710.8 ♂
SVL	73.3	69.7	73.8	73.7	75.1	85.7	75.1	75.6	69.0	48.6	50.0	43.9	42.0	42.8
AxialL	31.0	30.3	32.5	29.6	31.2	40.1	33.4	37.5	31.8	23.4	23.1	19.6	17.1	18.5
TailL	71.6	76.0	reg.	72.7	reg.	reg.	reg.	reg.	reg.	49.5	51.0	42.0	43.6	reg.
ArmL	25.5	26.1	25.9	25.0	25.7	31.5	27.2	25.3	24.4	17.3	16.8	15.8	12.3	14.1
LegL	33.6	32.0	32.1	31.7	36.5	36.2	35.6	34.5	31.3	23.8	22.5	20.5	18.6	19.9
HeadL	20.0	19.0	20.6	20.5	20.9	22.1	21.7	21.8	18.4	13.8	14.7	12.9	12.7	12.4
HeadW	14.0	13.5	13.7	14.1	14.5	16.2	14.2	14.0	13.2	9.9	9.9	8.1	8.0	8.2
HeadH	8.7	8.5	9.2	9.3	8.5	10.7	9.8	9.4	7.9	6.2	6.5	5.4	5.6	5.7
SnoutL	8.0	7.8	8.3	8.5	8.1	9.2	8.3	8.8	7.6	5.5	6.1	5.3	4.8	5.1
OrbD	4.8	3.9	4.1	4.4	4.4	4.9	4.7	4.1	3.7	3.4	3.1	3.2	2.9	2.9
DTR	11	17	16	13	17	19	15	13	15	15	17	18	18	-
PVT	26	24	26	28	22	24	26	25	23	25	26	29	26	27
VS	46	40	42	38	38	40	34	45	41	39	37	-	43	38
PFS	57	55	59	52	50	51	50	54	52	49	51	-	-	42
PFP	56	52	57	49	45	0	45	50	0	24	?	26	-	43
PP	n/a	n/a	n/a	n/a	n/a	20	n/a	n/a	16	n/a	18	n/a	-	n/a
FP	n/a	n/a	n/a	n/a	n/a	9/9	n/a	n/a	11/9	n/a	n/a	n/a	-	n/a
InfraS	n/a	n/a	n/a	n/a	n/a	1/3	n/a	n/a	2/1	n/a	?	n/a	n/a	n/a
PCT	1	2	1	1	2	2	2	3	3	2	2	1	2	2
SupraLab	9	8	10	13	9	10	10	10	10	10	12	10	9	11
InfraLab	9	9	9	9	9	10	9	9	7	9	9	9	9	8
SC	31	30	29	33	27	34	32	31	30	27	30	35	31	31
IOS	47	46	-	38	44	45	51	43	39	49	48	-	46	42
GulS	6	6	6	8	5	9	6	8	6	8	7	8	7	6
LT4	22	20	20	20	18[a]	19[a]	22	22	21	23	21	22	17[a]	21

[a] Following Hartmann *et al.* (2016) we counted subdigital scales underneath the fourth toe beginning with the first notably enlarged/ transversely widened scale (lamellae), which is usually located at the toe joint. In three specimens with < 20 subdigital scales, a few of the proximal scales were fragmented (or similar to plantar scales). If these are included in the count, the following values are obtained: 2710a.5 = 21 LT_4, 2710a.6 = 22 LT_4, 2710.7 = 20 LT_4.

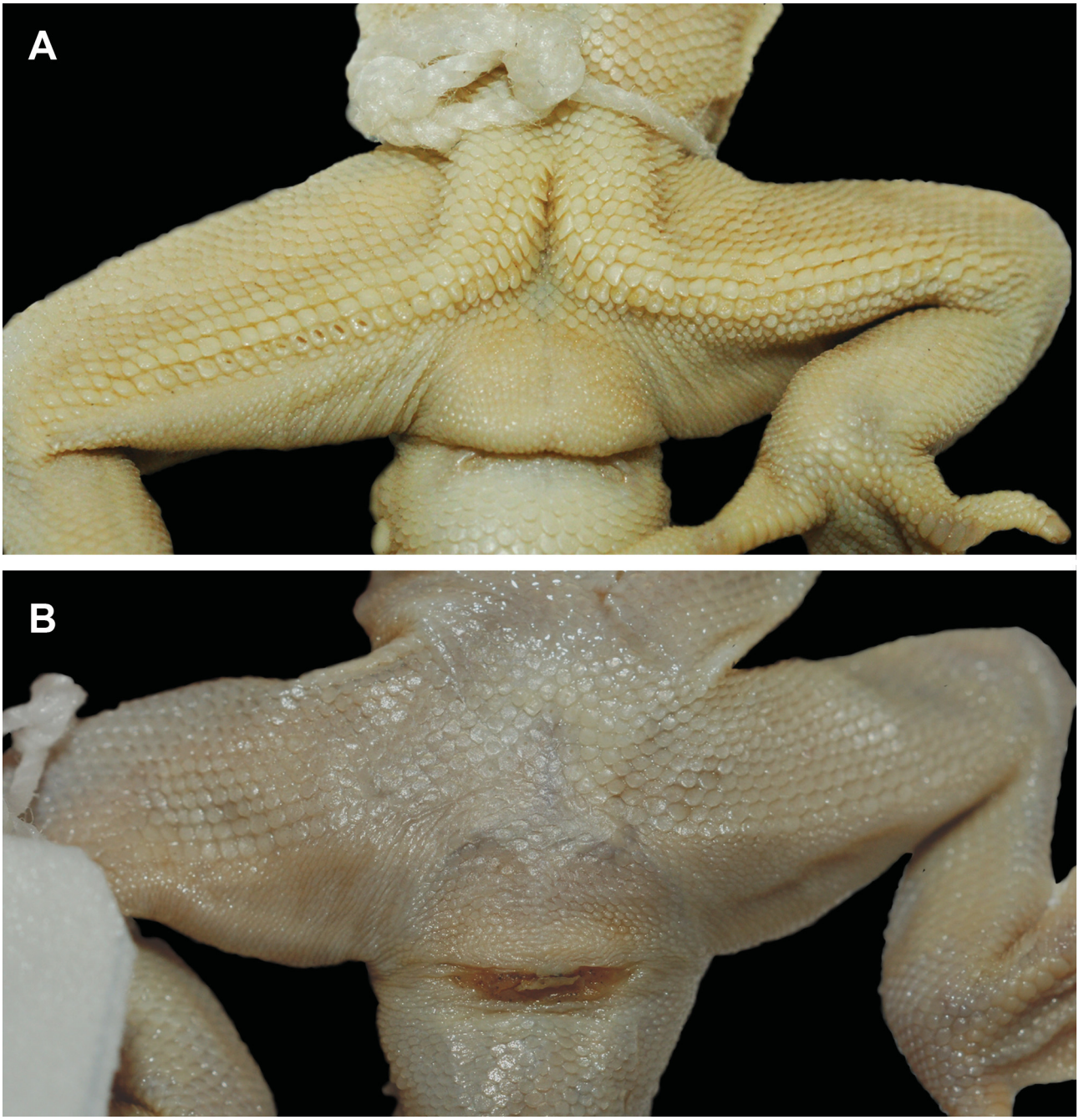

FIGURE 1. Precloacal region of *Cyrtodactylus marmoratus*. (A) Lectotype of *C. marmoratus* (RMNH.RENA. 2710a.1; adult male) with a precloacal groove as typical for males of that species. (B) Paralectotype of *C. marmoratus* (RMNH.RENA. 2710.3; adult female) lacking a precloacal depression as typical for females of that species. Photographs are not to scale. Plate prepared by Max Kieckbusch based on photographs by Sven Mecke.

Correction and update of the comparative table in Hartmann *et al.* (2016)

While our research on bent-toed geckos from the Sunda Islands, Sulawesi, and the Moluccas continues (Mecke *et al*. in press, in prep.), we noticed some inaccuracies in our previously published comparative table (Hartmann *et al*. 2016: Table 3), pertaining largely to the presence/absence of a precloacal depression in males *vs*. females. We herein correct these inaccuracies and take the opportunity to complement the earlier table by including the recently described *Cyrtodactylus hitchi* Riyanto, Kurniati & Engilis, 2016 and *C. petani* Riyanto, Grismer & Wood, 2015, and by adding new data for several species (e.g., *C. jellesmae* [Boulenger, 1897] and *C. marmoratus*). Furthermore, we here exclude the following characters from our table: tubercles on hind limbs and tubercles on head. A re-

evaluation of the literature cited in the reference section and a re-examination of relevant bent-toed gecko specimens revealed that tubercles are invariably present on the head (at least on the occiput) and the hind limbs of *Cyrtodactylus* from the Sunda Islands and Sulawesi. Thus, these characters are of no importance for diagnosis and/or taxonomy. The presence/absence of tubercles on the upper arm (brachium) seems to be a more important character for differentiating species than the tuberculation of the whole forelimb, since tubercles on the forearm (antebrachium) are usually present. Hence, we exchanged 'tubercles on forelimbs' for 'tubercles on the upper arm (brachium).' We also ascertained that only adult specimens were included in our comparison. Lastly, we supplemented our table by adding a column to provide information on the distribution of the species involved. Below we present a corrected and updated comparative table (Table 2) for the bent-toed geckos of the Sunda Islands and Sulawesi.

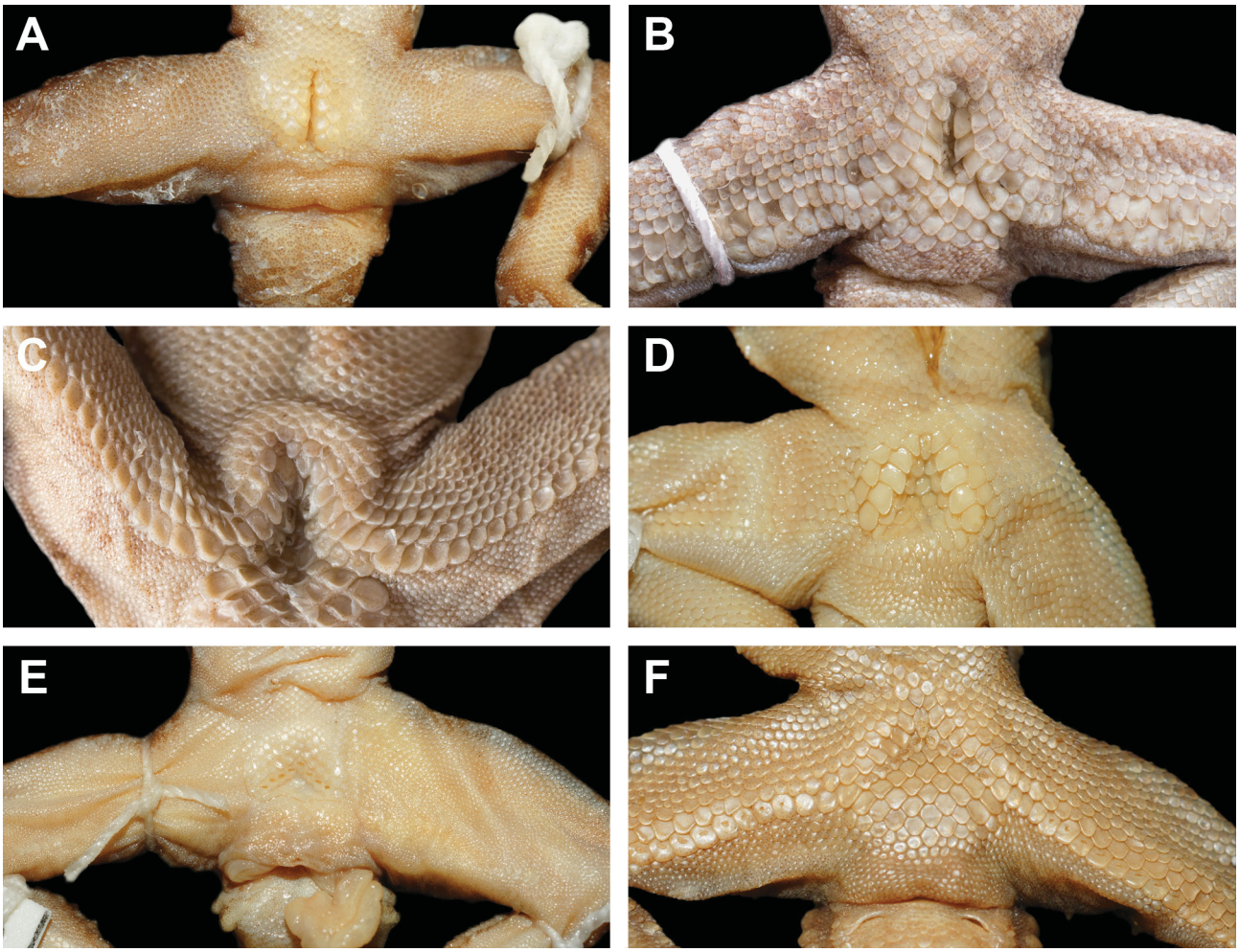

FIGURE 2. Precloacal regions of six Sundanese and Sulawesi species of *Cyrtodactylus* showing differences in the expression of a precloacal depression in adult males. (A) *C. pubisulcus* (AMNH R111889) possessing a slit-like precloacal groove, with the pore-bearing scales sunk deeply into the depression and not visible. (B) *C. klakahensis* (SMF 22476; holotype) possessing a slit-like precloacal groove, with the pore-bearing scales sunk deeply into the depression and barely visible. (C) *C. fumosus* (BMNH 1896.12.9.3) possessing a precloacal groove, with the enlarged pore-bearing scales arranged in the shape of an inverse 'Y' with the groove broadening posteriorly. (D) *C. baluensis* (MCZ.Herp R-39036) possessing a precloacal pit, with the pore-bearing scales from the left and right side of the posterior-most precloacal scale series arranged in the shape of an inverse 'V' and widely separated from each other, creating a depression in the form of an acute triangle. (E) *C. consobrinus* (MCZ.Herp R-102031) possessing a precloacal pit in the form of an obtuse triangle. (F) *C. wetariensis* (AMNH R32165; holotype) lacking a precloacal depression. Photographs are not to scale. Plate prepared by Max Kieckbusch based on photographs by Sven Mecke.

TABLE 2. Characters used to distinguish *Cyrtodactylus* species occurring in the Sunda Islands and Sulawesi. The presence of a diagnostic character is coded as '1', the absence of a character is coded as '0'. For taxa possessing precloacofemoral scales (= scales in a continuous series; column entitled '7'), precloacal- and femoral scales (separated from each other by infrascales) are coded as 'n/a' (columns entitled '5' and '6'). Numbers at the head of the table correspond to characters as follows: 1 = tubercles on upper arm (brachium), 2 = number of ventral scales, 3 = enlarged subcaudals, 4 = number of subdigital scales/lamellae under 4th toe, 5 = enlarged precloacal scales (the number of pores is given in parentheses and includes primordia; if pores are present in one sex only, this is indicated either by '♂' or '♀'), 6 = enlarged femoral scales (the number of pores is given in parentheses and includes primordia; if pores are present in one sex only, this is indicated either by '♂' or '♀'), 7 = enlarged precloacofemoral scales (the number of pores is given in parentheses and includes primordia; if pores are present in males only this is indicated by '♂'), 8 = precloacal and femoral pores in a continuous series, 9 = expression of precloacal depression (N = no depression, G = groove, P = pit; if a depression is present in males only, this is indicated by '♂'), 10 = pattern of dorsum (bd = banded; bl = blotched; mo = mottled; pl = patternless; st = striped). If data for a character are not available, this is indicated by a question mark (?). The abbreviation 'Dist.' stands for 'Distribution' and indicates the island(s) on which a respective taxon occurs. Where derived from the literature ('Lit.' column), references are abbreviated by letters as follows: A = this publication; B = Rösler *et al*. 2007; C = Youmans & Grismer 2006; D = Manthey & Grossmann 1997; E = Hikida 1990; F = Iskandar *et al*. 2011; G = Inger & King 1961; H = Kathriner *et al*. 2014; I = Rösler & Kaiser 2016; J = De Rooij 1915; K = Brongersma 1934; L = Boulenger 1897; M = Das 1993; N = Riyanto *et al*. 2016; O = Malkmus *et al*. 2002, P = Auffenberg 1980; Q = Darevsky 1964; R = Werner 1896; S = Harvey *et al*. 2016; T = Das 2010; U = Riyanto *et al*. 2015; V = Harvey *et al*. 2015; W = Inger 1958; X = Riyanto *et al*. 2014; Y = Linkem *et al*. 2008; Z = Taylor 1962; Aa = Grimser *et al*. 2012; Ab = Hayden *et al*. 2008; Ac = Dunn 1927. Under the column heading '*n*' we provide the number of adult specimens we examined personally.

Taxon	SVL (mm)	1	2	3	4	5	6	7	8	9	10	Dist.	Lit.	*n*
agamensis	50	0	67	?	26	n/a (?[a])	n/a (?[a])	1 (?[a])	?	G (♂)[a] ? (♀)	bl	Sumatra	A, B	1
baluensis	71–95	0/1	36–46	1	19–23	1 (9–11, ♂; absent or indistinct in ♀♀)	1 (4–10, ♂)	0	0	P (♂)	bd, bl	Borneo	A, C, D, E	8
batik	103–113	1	48–57	1	24–27	1	0	0	0	N	bd	Sulawesi	F	-
cavernicolus	64–81	0	51–58	0	22–26	1 (4, ♂)	0	0	0	G (♂) ? (♀)	bd	Borneo	C, E, G	-
celatus	38−44	0	34–42	0	15–18	1 (4, ♂)	0	0	0	G (♂)	bl	Timor	A, H, I	3
consobrinus	97–125	1	58–71	1	22–28	1 (8–11, ♂; absent or indistinct in ♀♀))	1 (0–6, ♂); 0/1 ♀	0	0	P (♂) ? (♀)	bd, mo	Sumatra, Borneo	A, C, D, E	2
darmandvillei	80−82	1	34–36	1	23−24	n/a	n/a	1	0	N	bl	Flores, Rinca, Komodo	A, J, K	2
fumosus	57–78	0	37–50	1	17–23	n/a (10–11, ♂)	n/a (3, ♂)	1	0	G (♂)	bl	Sulawesi	A, L	4
gordongekkoi	71–73	0	30	0	22–23	n/a	n/a	1	0	N	bl	Lombok	A, M	2
hitchi	62–79	?	39–45	1	18–21	1	0	0	0	N	bd	Sulawesi	N	-
ingeri	65–76	?	40–43	1	23–29	1 (7–9, only ♂♂ known)	0	0	0	N	bd, bl	Borneo	C, E, O	-
jellesmae	58–70	0/1	40−54	0	16–23	1	0	0	0	N	bl	Sulawesi and offshore islands[b]	A, F, L	9
klakahensis	61–68	0	35–38	0	17–20	n/a	n/a	1 (37–38, ♂)	1	G (♂)	bl	Java	A	3
laevigatus	38–47	0	30–34	0	10–15	?	0/1	?	0	N	mo, pl	Flores, Komodo	A, F, P, Q	5

...continued on the next page

TABLE 2. (Continued)

Taxon	SVL (mm)	1	2	3	4	5	6	7	8	9	10	Dist.	Lit.	*n*
lateralis	65–93	1	51–66	0	18–24	1 (9–13, ♂) (0–15, ♀)	0/1	0	0	G (♂)	bl	Sumatra	C, D, R, S	-
malayanus	70–83	1	58–62	1	21–23	1 (8–10, ♂)	0	0	0	P?	bd	Borneo?	C, E, J, T	-
marmoratus	69–86	0	34–47	0	18–24	n/a (16–20, ♀)	n/a (9–11, ♀)	1 (43–57)	0 (♀)/1	G (♂)	bl	Java	A, B	14
matsuii	105	?	48–51	0	22	0 (7–8, ♂)	0	0	0	N	bd, bl	Borneo	C, E, O, T	-
petani	45–57	0	30–35	0	17–18	n/a	n/a	1 (31–35, ♂)	1	N[c]	bl	Java	U	1
psarops	?[d]	0/1	38–49	0	18–22	n/a (?[e],♀)	n/a (?[e],♀)	1 (28–32, ♂) (0–29,♀)	0 (♀)/1	P (♂)	bd, bl	Sumatra	V	1
pubisulcus	56–74	0	37–58	0	16–23	1 (7–9, ♂)	0	0	0	G	bd, bl, st	Borneo	A, C, E, W	8
semiadii	40–47	?	35–36	0	14–15	0	0	0	0	N	bl	Java	X	-
semicinctus	?[d]	0	33–44	0	19–22	n/a	n/a	1 (36–38, ♂) (0–19,♀)	1	G (♂)	bd, bl	Sumatra	V	-
spinosus	70–83	?	38–44	0	19–21	1 (12–13, ♂)[f]	1 (?[g])	0	0	P (♂)	bd	Sulawesi	Y	
quadrivirgatus	51–71	1	34–42	0	19–20	n/a (0–4)[h]	n/a	1	0	N	bl, st	Sumatra	C, D, Z, Aa	-
wallacei	92–114	1	45–49	1	17–25	1	0	0	0	N	bd, bl	Sulawesi	Ab	-
wetariensis	58–67	0	36–38	0	20–22	n/a (11, ♂)[i]	n/a (12–16, ♂)[i]	1	0	N	bl	Wetar	A, Ac	3
yoshii	75–96	1	50–58	0	25–30	0 (8–12, ♂; absent or indistinct in ♀♀)	0	0	0	P(♂)	bl	Borneo	C, E	-

[a] While visiting the RMNH, we discovered in the herpetological collection a male specimen of *C. agamensis*. This is only the second specimen known of that species, with a detailed description of the female holotype provided by Rösler *et al*. (2007). We did not examine the male specimen in detail (i.e., we did not gather metric and meristic data), but we can certainly report the presence of a precloacal groove. Pores were present as well, but we are unfortunately not able to report on their expression (e.g., a continuous or discontinuous series).
[b] *C. jellesmae* occurs as far north as Talaud (Koch *et al*., 2009).
[c] Riyanto *et al*. (2015) provided inconsistent data on whether a precloacal groove is present in male specimens of *C. petani*. However, Awal Riyanto (in litt.) confirmed that male *C. petani* lack a precloacal groove or pit, as is also evident from their Fig. 4A.
[d] Harvey *et al*. (2015) did not provide ranges for adult specimens of *C. psarops* and *C. semicinctus*.
[e] In female *C. psarops*, pores (primordia) can either be arranged continuously, discontinuously, or can be absent altogether. Harvey *et al*. (2015) only provided counts for total pore numbers, but failed to indicate individual counts for the pore-bearing parts of separated pore series.
[f] In their diagnosis and Table 1, Linkem *et al*. (2008) listed 12–13 precloacal pores for *C. spinosus*, whereas in their Table 2 they listed only 8–12 precloacal pores. In their Table 1, these authors also listed precloacal pores for individual females, although females are described as lacking pores in their variation section.
[g] According to the diagnosis in Linkem *et al*. (2008), *C. spinosus* lacks femoral pores; it was listed as possessing 4–7 femoral pores in their Table 2.
[h] Taylor (1962), in his description of *C. quadrivirgatus*, reported males and females to usually possess four precloacal pores or primordia but failed to indicate if a sexual dimorphism for this character exists. Manthey & Grossmann (1997) reported the presence of three or four pores in males only, whereas e.g., Youmans & Grismer (2006) and Grismer *et al.* (2012) provided a range of 0–4 precloacal pores for the species, again without reporting on the likely occurrence of a sexual dimorphism.
[i] A female specimen (MCZ Herp R-26998), also collected by the Douglas Burden East Indian Expedition (1926), has nine precloacal pores, and no femoral pores on the right and two on the left thigh.

Variation in the pore series of adult *Cyrtodactylus marmoratus*

While all male specimens of *Cyrtodactylus marmoratus* we personally examined had a continuous pore series (precloacofemoral pores), female specimens appear to be more variable in this respect (Table 2). Of the five adult females examined, two had precloacal pores only (ZMA.RENA 15945, SMF 92361), in two specimens the femoral pores were separated from the precloacal pores by infrascales (RMNH.RENA 2710.3, 2710a.6; paralectotypes), and one specimen had a continuous series of pores (precloacofemoral pores; MTKD 8094). The pattern observed is similar to that reported for *C. psarops*, where adult male specimens possess continuous pore series, whereas female specimens show much variation in this character.

Brongersma (1953) also reported variation in pore and infrascale numbers in male specimens of *Cyrtodactylus marmoratus*, assuming this would be the result of an ontogenetic change. While ontogenetic variation or even variation in adult male specimens of this species appears to be possible, it is likely that Brongersma (1953) combined data from different Javanese taxa masquerading under the name *C. marmoratus*. Recent descriptions of new bent-toed geckos from Java (Riyanto *et al*. 2014, 2015; Hartmann *et al*. 2016) indicate that the diversity of this group of geckos in Java is largely underestimated.

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APPENDIX. Specimens examined for this study.

Cyrtodactylus agamensis.—**Indonesia**: no specific locality data available but collected by P. Bleeker, the describer of the taxon: RMNH.RENA 3965.

Cyrtodactylus baluensis.—**Indonesia**: *Kalimantan Timur Province*: "Mount Tibang" (= Bukit Batu Tiban): MCZ Herp R-22626.**—Malaysia**: *Sarawak* (*Borneo*): Mount Kinabalu (= Gunung Kinabalu): MCZ Herp R-39036; Mount Kinabalu: "Kaddmayan River", near Kiau: MCZ Herp R-43474; Kiau (= Kampung Kiau): MCZ Herp R-43477, R-163132; "Mahunbayon": MCZ Herp R-43473, R-163646; "Penokok River" (= alternative spelling of Kenokok River), near Kiau: MCZ Herp R-43476.

Cyrtodactylus celatus.—**Indonesia**: *Nusa Tenggara Timur Province*: West-Timor: Ofu: ZSM 556/2002, Soe: NMB-REPT 12789, "Djamplong, 55 kilometers by road from Kupang" ("Djamplong" = Tjamplong or Camplong): BMNH 1926.10.30.45 (holotype).

Cyrtodactylus consobrinus.—**Malaysia**: *Sarawak* (*Borneo*): Labang Camp on Sungei Seran, Bintulu District, Fourth Division: MCZ Herp R-102031; "Semerjoh Forest Reserve, First Division, 12.5 miles from Kuching": MCZ Herp R-160784.

Cyrtodactylus darmandvillei.—**Indonesia**: *Nusa Tenggara Timur Province*: Flores: Sikka: ZMA.RENA. 10943–44 (syntypes).

Cyrtodactylus fumosus.—**Indonesia**: *North Sulawesi Province*: "Bone Mountains" (= Pegunungan Bone): NMB-REPT 2662 (holotype); "Masarang": NMB-REPT 2663; Rurukan: BMNH 1895.2.27.7, 1896.12.9.3.

Cyrtodactylus gordongekkoi.—**Indonesia**: *Nusa Tenggara Timur Province*: Lombok: Vicinity of Sendanggila Falls, ca. 0.5 kilometers south of Senaru village: ZRC 2.3380 (holotype), ZRC 2.3381 (paratype).

Cyrtodactylus jellesmae.—**Indonesia**: *Central Sulawesi Province*: Malakosa, Kuala Navusu: AMNH R142969–70, 14296972–73; Tolai, Sungai River: AMNH R142974; *North Sulawesi Province*: Buol: NMB-REPT 2660 (lectotype); Mount Masarang: NMB-REPT 2661 (paralectotype); Pulau Biaro: MCZ 171466; *South Sulawesi Province*: Lowah (Muara Loa): MCZ 25337.

Cyrtodactylus klakahensis.—**Indonesia**: *Jawa Timur Province*: Lumajang, Klakah: SMF 22476 (holotype); SMF 22477–78 (paratypes).

Cyrtodactylus laevigatus laevigatus.—**Indonesia**: *Nusa Tenggara Timur Province*: Komodo: Loho Liang: FLMNH 28910–12.

Cyrtodactylus laevigatus uniformis.—**Indonesia**: *Nusa Tenggara Timur Province*: Flores: FLMNH 32596 (holotype), FLMNH 32597 (paratype).

Cyrtodactylus marmoratus.—**Indonesia**: Java: RMNH.RENA 2710.1–8 (paralectotypes), RMNH.RENA 2710a.1 (lectotype), RMNH.RENA 2710a.2–6 (paralectotypes), MTKD 8903–05; *Jawa Tengah Province*: "Goewa Djatidjadjar, Jdjoe, Bagelen" (= Gua Jatijajar, Kebumen): ZMA.RENA 15945; Karangpucung: SMF 92361

Cyrtodactylus petani.—**Indonesia**: *Jawa Timur Province*: "Toeloeng Agoeng" (= Tulungagung): ZMA.RENA 11353.

Cyrtodactylus psarops.—**Indonesia**: *Lampung Province* (*Sumatra*): "Wai Lima, Lampangs" (= Lampung): ZMA.RENA 14652

Cyrtodactylus pubisulcus.—**Malaysia**: *Sarawak* (*Borneo*): Baram River (= Sungai Baram): SMF 8223; Tubau Camp on Sungai Pesu, Bintulu District, Fourth Division: AMNH R111889–93, 111895; "Tandjong Datu", First Division (= Tanjung Datu National Park): MCZ Herp R-79197.

Cyrtodactylus wetariensis.—**Indonesia**: *Maluku Province*: Wetar: near Uhak, north coast of Wetar: AMNH R32164 (paratype), 32165 (holotype), MCZ Herp R-26998 (paratype)